2
What is Biodiversity?

Biodiversity includes not only the world's species with their unique evolutionary histories, but also genetic variability within and among populations of species and the distribution of species across local habitats, ecosystems, landscapes, and whole continents or oceans. Understanding what constitutes and defines biodiversity is essential for managers and policy-makers who must attempt to incorporate its values into their land- and water-management plans. It is only when we understand all the interacting scientific dimensions of biodiversity outlined in this chapter that we can appreciate the levels of information that must be considered. Biodiversity-management options are inevitably constrained by a combination of biological and sociopolitical realities. In this chapter, we present our biological understanding of biodiversity, which provides the basis for further chapters 3 and 4, which consider the "uses" and "value" of biodiversity.

The word *biodiversity* is used in many ways. Economists and ecologists, ranchers and gardeners, mayors and miners all view biodiversity from different perspectives. When people discuss biodiversity, they often use it as a surrogate for "wild places" or "abundance of species" or even ''large, furry mammals". Yet from the viewpoint of those engaged in biodiversity-related sciences—such as population biology, ecology, systematics, evolution, and genetics—biodiversity has a specific meaning: "the variety and variability of biological organisms" (Keystone Center 1991; Noss and Cooperrider 1994; Wilson and Peter 1988). The Convention on Biological Diversity similarly defines biodiversity as the "variability among living organisms from all sources''. Those definitions are so broad that they can be clearly understood only by considering particular levels of biological organization—genes, species, communities, ecosystems, and even our planet.

Each level requires different methods of analysis, different modes of understanding, and, ultimately, different approaches to management. For managers, it is not just a matter of counting species or individuals. Managers must consider the role of biodiversity in the functioning of ecosystems and the effects of management and use of resources on ecosystem processes.

George Evelyn Hutchison (1965), one of the founders of modern ecology, wrote about the "evolutionary play in the ecological theater". This multilayered drama generates, sustains, shapes, and sometimes even diminishes biodiversity. Charles Darwin's reflections on species diversity underlay one of the most farreaching theories in the history of ideas: the theory of evolution by natural selection. His travels from England to the strikingly different landscapes of the New World left him awestruck and inspired. Whatever constitutes biodiversity, Darwin recognized that Brazil had a lot of it and certainly more than he left behind in an English midwinter. No modern biologist would disagree. Like Darwin, we often equate biodiversity with the number and novelty of the species present.

Species, Populations, and Genes

There is genetic diversity within species. If each species were reduced to one small population of genetically similar individuals, we would lose much biodiversity. As we move across a region, the species change, even if the numbers of species in different places might not; a forest and an adjacent grassland might contain almost entirely different assemblages of species, for instance. Moreover, the ecosystem processes in a grassland differ from those in the forest nearby.

A population consists of individuals of the same species that live in the same place and interact in various ways, including interbreeding. Populations of the same species living in different places can exchange members, but they often are genetically differentiated to some degree and the further they are separated from each other, the more distinctive they become. Metapopulations are groups of spatially separated populations that occur in patches of habitat across a landscape. Populations can become locally extinct in different habitat patches across a landscape; they infrequently exchange members, and when they do, the passage between local populations is generally hazardous and entails movement across inhospitable habitat. Local populations that make up a metapopulation experience extinction, and habitat left open is recolonized at some finite probability by other local populations within the metapopulation.

The genetic variability among individuals within a species can result from gene recombination or mutation, genetic polymorphism (the presence of different forms of the same gene), isolation of gene pools, local selection pressures, habitat (environmental) complexity, landscape mosaics, and environmental gradients. Specific genetic combinations in populations result from natural selection acting on individuals in response to biotic and abiotic environments and from random, nonselective fixation of genes.

New developments in the study of molecular evolution and modern laboratory techniques make it possible to determine the degree or closeness of relationships within and between populations (Avise 1994, 1995; Hillis and others 1996). Molecular data and traditional anatomical information permit us to deduce phylogenies—the branching patterns of genealogical lineages and ancestry of sets of species (Hillis and others 1996).

Genetic Diversity and Adaptation

Much genetic variation is detectable only biochemically, but some is evident as variation in anatomy, physiology, behavior, and life-history characteristics—phenotypes—of individuals in a population. Genetic variation is the basis of local adaptations and of common phenomenon of gradual change in phenotype along a geographic transect where the environment changes. Genetic variation is also the basis of coevolution, whereby species evolve adaptations in response to each other's adaptations.

There are many examples of adaptive evolution within species. Across the extensive continuous range of the common mussel off the eastern coast of North America, despite its enormous reproductive output and high rates of genetic exchange, populations are genetically differentiated over surprisingly small distances—from a few meters to several kilometers (Koehn and Hilbish 1995). The common yarrow, a composite plant from California, is able to live over a great range of habitats, from the high Sierra Nevada to the Pacific Coast, and shows distinctive, genetically determined forms in different habitats (Clausen and others 1958). *Drosophila* flies show extensive variation in genome organization according to habitat, elevation, regional geography, and seasonality (Dobzhansky 1970).

Effective environmental management includes considerations of genetic variation. For example, salmon stocks in different rivers in the same region exhibit differences in genetic makeup. These are the result of independent evolution of distinct stocks, each of which has adapted to local conditions. The differences seen reflect the histories of the stocks, some resulting from local selection pressures and others from the accumulation of random changes associated with the degree of isolation and population size.

Genetic diversity provides an economic basis for protecting and conserving biodiversity (McNeely and others 1990; Oldfield 1984; Potter and others 1993; Reid and Miller 1989; Reid and others 1993; WRI/IUCN/UNEP 1992). For example, Douglas fir trees grow abundantly across the western United States. Their success is due to their diversity despite their similar appearance (Rudolph 1990). Coastal and interior populations show genetic differences in cold hardiness, response to moisture stress, and timing of bud bursts. There are also genetic differences between populations only 3–10 km apart that are exposed to different microclimates on north-facing and southfacing slopes. Moreover, genetic variability results in the continued production of diverse phenotypes, some of which are more able than others to resist attacks by western spruce budworm, an important pest for this species. Commercial nurseries make use of local variation in reforestation programs.

Current adaptations are important, but genetic diversity is also critical for the future resilience and persistence of natural systems. Variation is important to maintain a population's ability to respond to changing environmental conditions, whether natural or anthropogenic. A notable example is the rapid adaptive evolution of plants that have colonized mine tailings that are polluted by heavy metals in Great Britain (Antonovics and others 1971). This represents natural evolutionary potential, which can be particularly important in the face of rapid global change.

For managers of biodiversity, there are practical implications in the observations that some species have many locally distinct populations but others show little geographic variation and that some species have no close relatives but others occur in genera that include hundreds of species. Biologists have recognized that current taxonomy (the classification of organisms on the basis of the evolution of species from their ancestors) is sometimes inadequate for identifying appropriate units for conservation. They have recommended counting "evolutionarily significant units" (ESUs) (Moritz 1994; NRC 1996), historically isolated parts of species that, in addition to representing divergence and diversification in the past, can have direct evolutionary potential. Focusing on ESUs has the goal of ensuring that evolutionary heritage is recognized and protected.

Measures of Diversity

One of the decisions that managers face is how to assess biodiversity. How do we know whether biodiversity has changed? Scientists use different methods to assess biodiversity.

Biodiversity among areas can be compared with statistical indexes of species diversity (Magurran 1988; Pielou 1975). Most indices combine two different metrics: the total number of species and the relative abundances of all species (evenness) in a sample. Such indexes have been criticized on the grounds that similar values of an index might reflect quite different sample compositions. A given index value could reflect a high species richness (a large number of species, many of them rare) or could be attributed to many fewer but commoner species (for example, high relative abundance of many species).

The simplest measure of diversity, the number of species in a given area, is called within-area diversity or, technically, alpha diversity. Ecologists generally call this measure species richness; they imply no economic value by using *rich* or its opposite, *poor*. Only their presence (not their abundance) is taken into consideration in counting the number of species in an area.

Species counts are the most visible and most widely known measures of biological diversity. Tourists visit Costa Rica in part because its forests are so rich in bird species and its marine reefs are so rich in corals and fishes (see Costa Rica case study below). The biodiversity of the Camp Pendleton region in southern California includes 345 vertebrate species, a high level that constitutes a large percentage of all terrestrial vertebrates in that richly diverse state. The preeminence of the species as the central unit of biodiversity is explicit in the Convention on Biological Diversity (Heywood 1995; UNEP 1992) and the UN Environment Program's Explanatory Guide to the Convention (Glowka and others 1994). Although simple species-per-area statistics are useful, there are caveats:

Species counts are rarely complete.
Counts depend in complex ways on the area surveyed and how the survey was conducted.
Counts of individual species might need to be weighted by their abundances, percentage covered, or mass.

Surrogate measures of biodiversity, such as the numbers of genera (the taxonomic category directly above the species in the Linnean hierarchy) or even higher taxa (such as families), have been used. These can be effective when taxonomy accurately reflects underlying relationships and includes the descendants of a common ancestor, but systematists recommend that such approaches be treated with care and considered to be only interim stages in the development of a deeper understanding of biodiversity.

If phylogenetic analyses are available, it can be useful to estimate the number of lineages present to take into consideration uneven species representation. For example, 20 species of lizards might represent only three main lineages in one area, but 15 in another. Such information might be used to identify a focus of active evolutionary diversification in the first case and the survival of ancient lineages in the second. Such tentative conclusions gain force if additional instances of coexisting taxa are found.